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The Population Dynamics of the Norway Pout in the North Sea

By D. F. S. RAITT
Marine Laboratory, Aberdeen
May 1968

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The Population Dynamics of the Norway Pout in the North Sea

INTRODUCTION

A programme of research into the life history and general biology of the Norway pout, *Trisopterus esmarkii* (Nilsson 1855), has been carried out at the Marine Laboratory, Aberdeen, since 1960. The available literature on the biology and population dynamics of this species has been reviewed in one of a series of synopses of fish produced by the Food and Agriculture Organization of the United Nations (Raitt, 1966). Initially the work was designed to delimit the stock of Norway pout in the northern North Sea (Raitt, 1965), to attempt to determine the position and importance of Norway pout in the food cycles of the northern North Sea (Raitt and Adams, 1965) and to describe the distribution and abundance of Norway pout (Raitt and Mason, 1968). In this last report it was shown that the routine surveys carried out in the northern North Sea by the research ships of the Department of Agriculture and Fisheries for Scotland cover the area of maximum abundance of Norway pout in this region. Recent investigations have been concentrated mainly on the population dynamics of the northern North Sea stock. The results of this research are described in the present paper.

The author gratefully acknowledges the help and advice of Dr C. E. Lucas, Mr B. B. Parrish and Prof. V. C. Wynne-Edwards. In addition, thanks are due to Mr W. B. Hall for carrying out the statistical analyses of the fecundity data.

MATERIAL AND METHODS

During the years 1960–66 the research vessel "Scotia" carried out regular routine trawling surveys over the northern North Sea in the spring (March–April), summer (June–July) and autumn (September–November) (Table I). The gear used was a "Wing" trawl with a 70 ft headline and small-meshed codend. The area covered extended from latitude 57°N to 61°N and from longitude 2°W to 2°E. Wherever possible fish were sampled at every trawling station; at least 250–300 fish, taken at random, were measured to the nearest centi-

TABLE I

"SCOTIA" NORTHERN NORTH SEA SURVEYS, 1960–66, DATES OF CRUISES AND NUMBERS OF TRAWL HAULS

Year	Spring		Summer		Autumn	
	Dates	No. of hauls	Dates	No. of hauls	Dates	No. of hauls
1960	26/2–12/4	33	15/6–25/6	20	12/9 –28/9	31
1961	5/3–19/4	35	—	—	7/9 –22/9	27
1962	9/3–19/3	16	9/6–23/6	29	15/10–22/10	20
1963	21/3– 5/4	20	24/5–10/6	36	14/11– 5/12	20
1964	4/3–12/3	20	—	—	10/11–25/11	23
1965	15/3–30/3	21	3/6–21/6	27	6/10–28/10	20
1966	5/4–20/4	26	17/7–23/7	17	4/11–20/11	21

metre. From these fish, otoliths were collected from five fish in each centimetre group. The rest of the catch was counted, or if too numerous, estimated by counting the fish in one basket and multiplying by the number of baskets caught. When the ages of the fish in the samples had been determined by examination of the otoliths the age distribution of all the fish in each haul was obtained by simple proportion. The range of values of

mean length at each age between hauls in each survey was negligible, so all hauls were averaged to give a mean age-length distribution for each survey.

In addition to the detailed data referred to above, use was also made of the laboratory's past trawling records from North Sea surveys in the spring carried out by the old F.R.S. "Explorer" from 1930 to 1955 (except for the war years 1939–45).

AGE DETERMINATION

Scales were found to be of little use for age determination as they are easily rubbed off in the trawl. In the few scales examined, however, the rings were very clear and agreed in every case with the numbers of zones on the otoliths.

The otoliths of Norway pout have been described by Scott (1905), Saemundsson (1929) and Gokhale (1953). They are comparatively large, dense and thick, measuring from 6 to 10 mm in length. The method of examination adopted was that used by Rollefsen (1933) and Trout (1957) for cod otoliths, and Gambell and Mestorff (1964) for whiting otoliths. The otolith is broken transversely and a beam of light striking the side of the otolith is transmitted upwards through it, illuminating the opaque and hyaline zones on the broken face. Zones which are hyaline when viewed by direct light are opaque using this method, and opaque zones appear hyaline. The examination was made using a Beck binocular microscope fitted with $\times 10$ eye pieces and a 59 mm objective. This gave a magnification of approximately $\times 17$ and enabled the whole of the broken surface to be seen.

Confirmation of the validity of age determination has been obtained by examining, under direct illumination, the edges of the otoliths over a period of 14 months from March 1960 to April 1961. Although no samples were taken in November and February it is clear (Figure 1) that the majority of otoliths had an opaque edge from April to August and a hyaline edge from September to March. Thus the hyaline band is laid down once a year during the winter as in other gadoids.

The zones on the otoliths of Norway pout were found to be very distinct. Gokhale (1953) surveyed the literature on Norway pout and concluded that in the North Sea the spawning period occurred from January to April (see also Raitt, 1965). For the purposes of this investigation the "birthday" of the fish was taken as 1st January so that during the March–April surveys all fish with one winter zone were assigned to the I-group (1-year-old fish). These fish showed one winter zone, either on the edge of the otolith or bounded by a narrow opaque zone representing the start of the second year's growth. Fish with two zones were II-group (2-years-old) and so on.

AGE DISTRIBUTION AND ABUNDANCE

In Figure 2 the percentage distributions of the different age-groups are shown for all the "Scotia" surveys from 1960 to 1966 (Table I). It can be seen that the Norway pout is a short-lived species, very few individuals being found over four years of age. This is in agreement with the findings of other North Sea workers. In the spring and summer 1-year-old fish consistently predominate in the samples. Apart from 1963 they made up from 65 to 98% of the total. In 1963, however, only 40% of the total number of fish in the spring survey were one year old, and they were in fact outnumbered by the 2-years-old fish for the first and only time in six years of sampling. This was also shown in the 1963 summer survey, but by the time of the autumn survey the relative abundance of the different age-groups was the same as in other years. The 1962 year-class, therefore, appears to have joined the fishable stock rather later than usual.

The autumn histograms also show the O-group fish of the brood spawned in the spring of the same year appearing for the first time. In 1966 this new brood accounted for more than 65% of the population sampled.

For a more precise estimation of the differences between years it is necessary to consider the actual numbers caught, and these data are given in Figure 3 as the average catch per hour's trawl haul during the

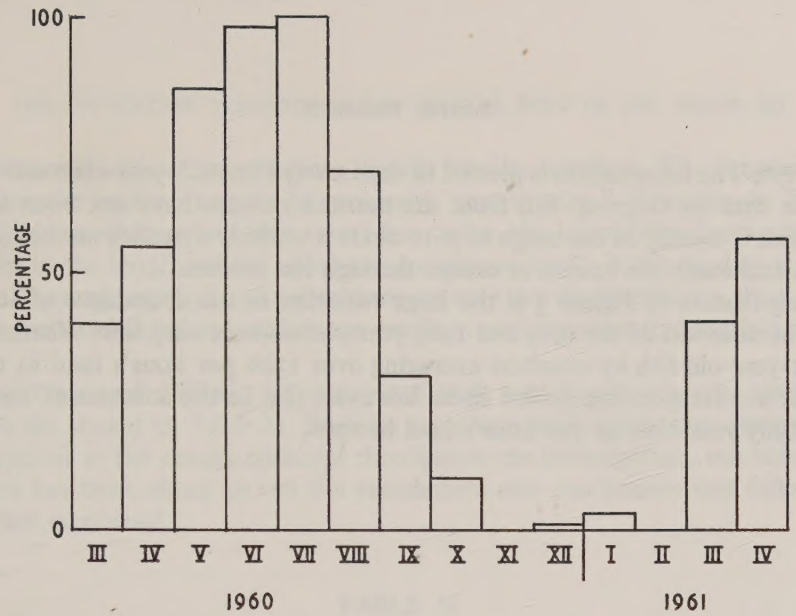

Fig. 1. Percentage of otoliths with an apaque edge, March 1960–April 1961.

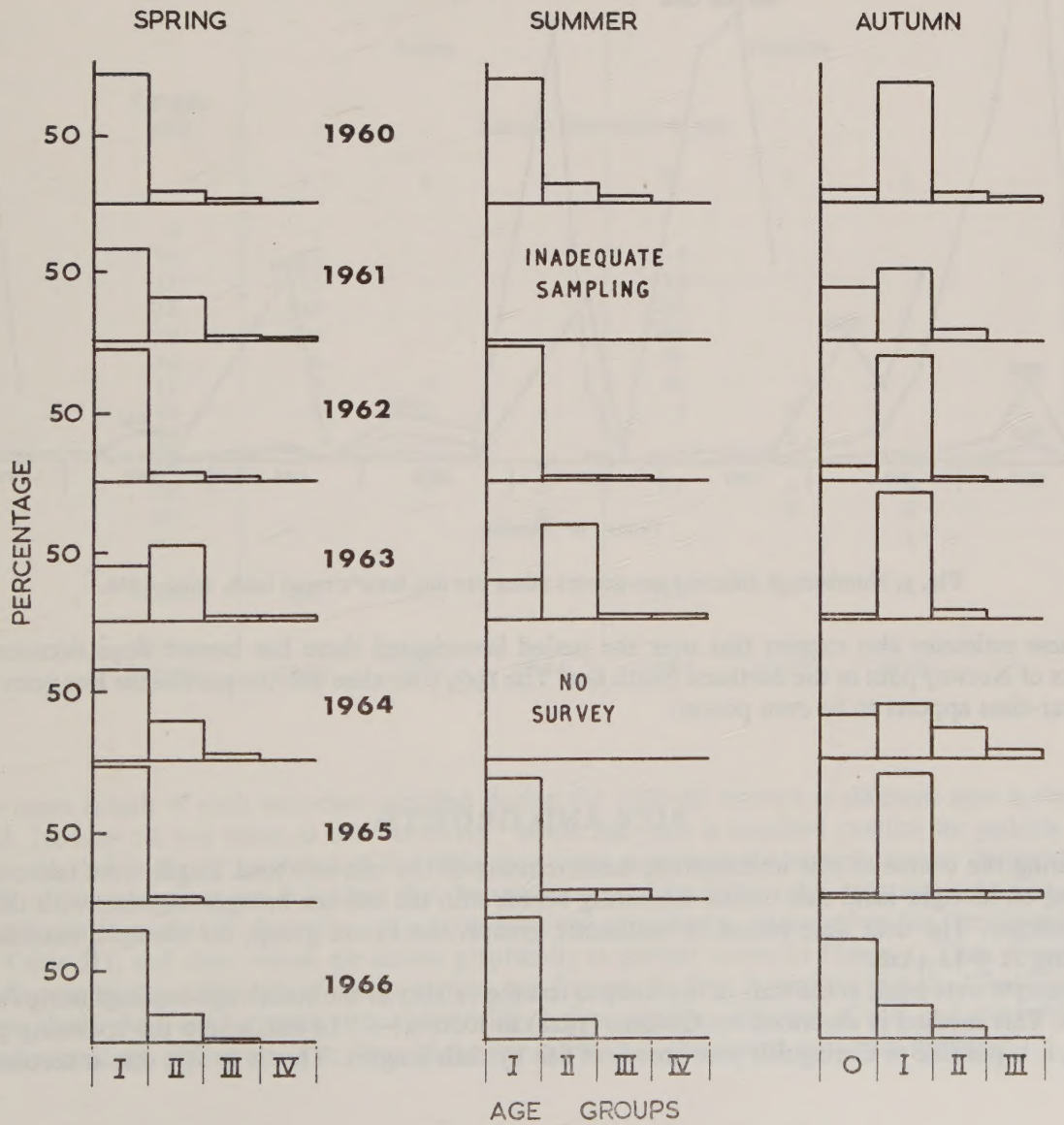

Fig. 2. Percentage age-composition during routine surveys 1960–66.

routine trawling surveys. The information is plotted in such a way that each year-class can be followed throughout its life-span. The data on O-group fish from the autumn surveys have not been included. As the size distribution of these fish is usually in the range of 5–10 cm it is unlikely that they are being adequately sampled by the trawling gear, and many are known to escape through the meshes.

The most striking feature of Figure 3 is the large variation in the abundance of successive year-classes during the period. The numbers of the 1963 and 1965 year-classes were very low. Whereas the 1959 year-class was represented as 1-year-old fish by numbers averaging over 1300 per hour's haul in the summer of 1960, the 1963 year-class at a corresponding period in its life cycle (i.e. in the summer of 1964) averaged only 60 individuals and the 1965 year-class 48 per hour's haul in 1966.

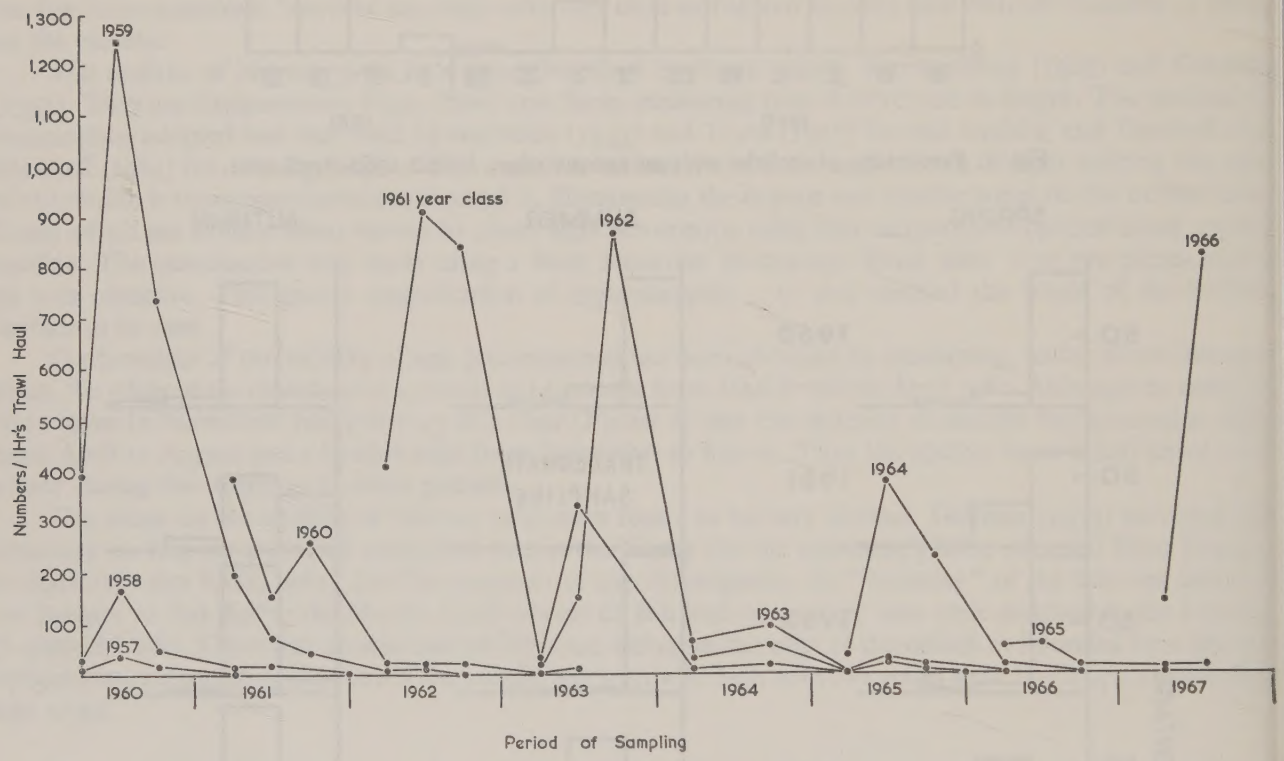

Fig. 3. Numbers of different age-groups taken per one hour's trawl haul, 1960–1966.

These estimates also suggest that over the period investigated there has been a large decrease in the numbers of Norway pout in the northern North Sea. The 1963 year-class was the poorest for five years and the 1965 year-class appears to be even poorer.

SIZE AND GROWTH

During the course of this investigation measurements of the extreme total length were taken with the fish lying on its right-hand side on the measuring board, with the tail fins brought together with the thumb and forefinger. The data were placed in centimetre groups, the 12 cm group, for example, containing fish measuring 11·5–12·4 cm.

Attempts were made at the start of the study to test the validity of the otolith age-readings using Petersen's method. This method is described by Graham (1928) as follows:— "In fish where the spawning period is limited, it is possible to distinguish year-broods of fish by their lengths. That is to say, that at certain lengths

a large number of fish are found, at intermediate lengths smaller numbers. The lengths at which the larger numbers are found are the average lengths of successive year-broods." However, in Norway pout, with a probable maximum life span of four, and very rarely five, years, the length-distribution curve flattens early in life and the differences in the lengths of the older age-groups are small. It can be seen in Figure 4, based on data from the "Scotia" spring survey of 1960, that there are only two distinct modes, the first coinciding exactly with that found for 1-year-old fish from otolith age-readings and the second comprising a mixture of 2- and 3-years-old fish.

The length distributions of different age-groups of male and female Norway pout from the "Scotia" survey of March 1962 are shown in Table II. Females are consistently larger than males in each of the three age-groups. This is typical of the results obtained throughout the investigation, but since the sex ratio of all the samples examined has been about 50 : 50 the calculations and conclusions that follow are based on data for male and female fish combined.

TABLE II

AGE-LENGTH DISTRIBUTION OF MALE AND FEMALE NORWAY POUT, MARCH 1962

Length (cm)	Males			Females		
	Length frequency at age					
	1	2	3	1	2	3
9	1					
10	14			5		
11	85			35		
12	220			137		
13	100			284		
14	9			82		
15	3	2		22		
16	2	12	1	7	5	
17		4			9	
18		3	4		11	2
19		2	1	1	9	2
20			1		6	6
21						1
Total	434	23	7	573	41	11
Mean Length	12·04	16·61	18·14	12·87	18·17	19·55

The mean length of each year-class sampled during the 1960–66 surveys at different ages is shown in Table III. January 1st was taken as the "birthday" of the fish (this is standard practice for gadoids in the North Sea) so that in the first column of the table, 0·75 years represents the autumn survey during the first year of life of the year-class, etc. It is clear that the size-for-age of the 1959, 1960, 1961 and 1962 year-classes is quite different from that of the 1963, 1964, 1965 and 1966 year-classes. Mean values for these two sets are given in Table III, and these values are shown graphically as growth curves in Figure 5. They demonstrate a fairly constant length difference of nearly 1·5 cm, age for age. In fact, it appears that the "fast" growing year-classes made their extra growth very early in life, before reaching one year of age, and thereafter have simply maintained the difference. The slope of the two curves, i.e. the growth-rate, was the same.

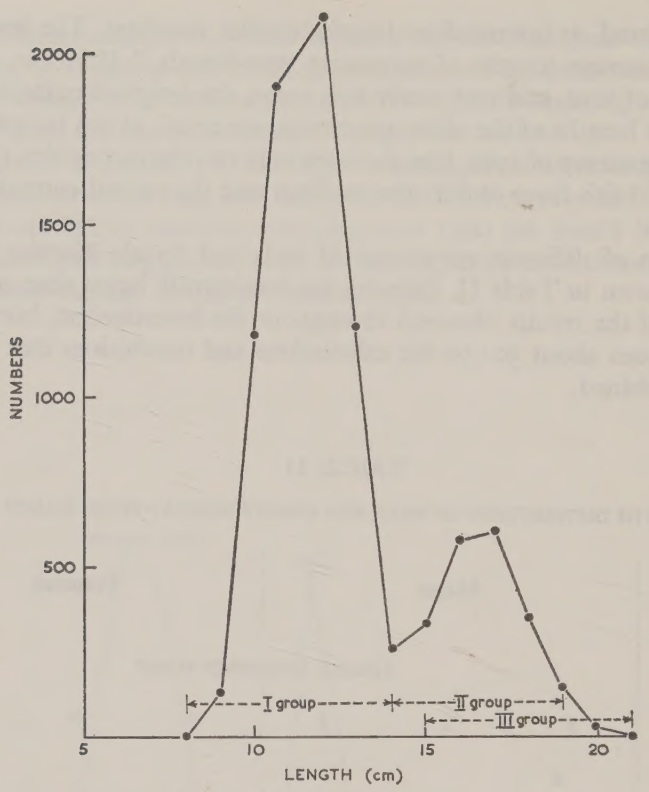

Fig. 4. Length distribution of Norway pout taken by "Scotia", March–April 1960.

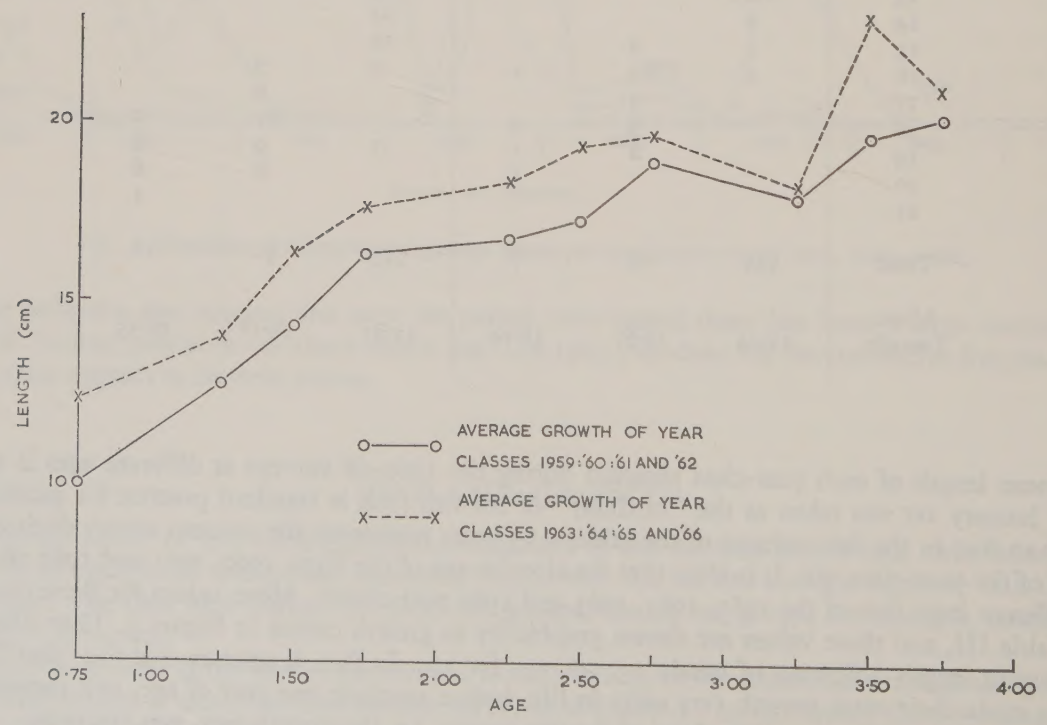

Fig. 5. Comparison of the average growth of the year-classes from 1959 to 1962 with those from 1963 to 1966.

TABLE III

MEAN LENGTH OF DIFFERENT YEAR-CLASSES AT VARYING AGES

Year-Class	Mean Length at Age (in years)									
	0·75	1·25	1·50	1·75	2·25	2·50	2·75	3·25	3·50	3·75
1959	—	12·30	14·36	15·67	16·02	16·84	18·93	18·75	19·58	20·00
1960	9·71	12·69	14·43	16·95	17·93	18·13	18·18	17·00	19·76	19·00
1961	9·37	12·65	14·60	16·07	16·60	16·79	19·09	17·94	—	21·08
1962	10·83	13·13	14·10	16·67	16·64	—	19·59	—	19·66	20·58
Average 1959–62	9·97	12·69	14·37	16·34	16·80	17·25	18·95	17·90	19·67	20·17
1963	12·48	13·66	—	18·17	18·92	19·27	19·74	18·17	23·00	21·00
1964	13·23	14·37	16·18	17·58	17·88	19·47	19·68			
1965	11·79	13·96	16·47	17·13						
1966	11·38									
Average 1963–66	12·22	14·00	16·33	17·63	18·40	19·37	19·71	18·17	23·00	21·00

Ursin (1963) carried out a detailed study of the growth of Norway pout from the Skagerrak and has already commented on the difficulty of fitting statistical growth curves to such short-lived, fast-growing species since there are wide seasonal variations in growth associated with varying temperatures and levels of feeding at different times of the year. The data in Table III and Figure 5 suggest that most of the increase in size occurs from the spring to the autumn and that there is relatively little growth between autumn and the following spring.

Furthermore, in a small short-lived species like Norway pout, the calculated mean lengths of fish less than 1-year-old (i.e. less than about 10 cm) are unduly influenced by mesh selection of the catching gear, and estimates of mean length at age 3 and over are influenced by the small numbers of fish of this age-group available for age determination.

Representation of the growth of fishes by mathematical equations has been described by, amongst others, Beverton and Holt (1957). The growth curve may be represented by an inverse exponential equation which, in its simplest form, is as given by von Bertalanffy (1938):

$$l_t = L_\infty(1 - e^{-Kt})$$

The following values of these parameters are obtained from the estimated lengths at ages 1, 2 and 3 and the method of fitting data to the von Bertalanffy growth curve described by Gulland (1964).

	L_∞	K
Average data for year-classes 1959–62	18·99	0·44
Average data for year-classes 1963–66	19·34	0·59

The value of the above results is strictly limited because of the shortcomings already discussed. Ursin (1963) found seasonal variations in his estimates of L_∞, for fish from the Skagerrak, from 9 to 27 cm and of K from 0·5 to 0·9. However, because of the large amount of data involved in Table III it can be concluded that the growth parameters for the two sets of year-classes do show significant differences. The occurrence of the apparently poor year-classes from 1963 to 1965 appears to have been in some way associated with a change in growth, and the 1963, 1964 and 1965 year-classes are larger at the same age than any of the other year-classes previously analysed for age and length.

LONG TERM FLUCTUATIONS IN ABUNDANCE AND ASSOCIATED CHANGES IN GROWTH

The abundance and growth of Norway pout in the northern North Sea have been studied from data collected during trawling surveys from 1930 to 1955 (excluding the war years). During this period the trawling surveys, on which "Explorer" worked a 48 ft otter trawl with a small-mesh cover, each year covered

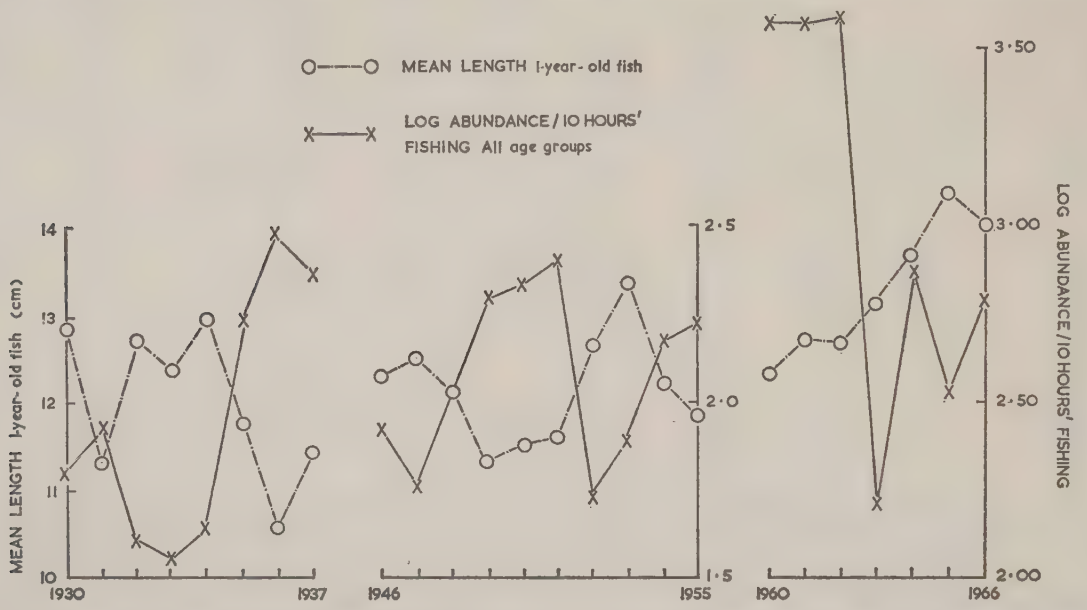

Fig. 6. Relationship of mean length of 1-year-old Norway pout to the overall abundance, 1930–37, 1946–55 and 1906–66.

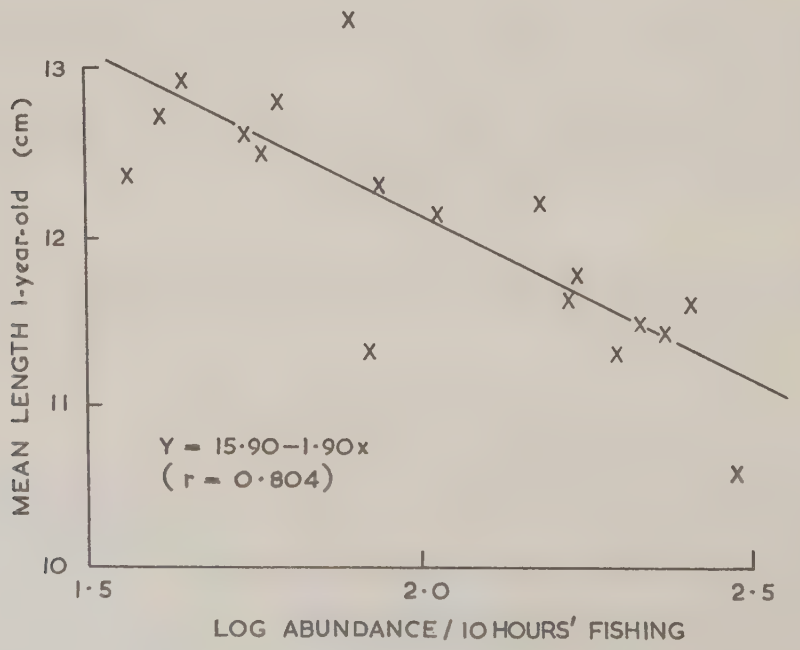

Fig. 7. Correlation of mean length of 1-year-old Norway pout with abundance.

roughly the same area extending from latitude 57°N to 61°N and from longitude 3°W to 3°E. Data from the surveys carried out by F.R.S. "Scotia" from 1960 to 1966 have also been used. These covered the same area in the northern North Sea although the gear employed was the "Wing" trawl with a small-mesh codend but no cover. The spring surveys (March–April) were chosen for analysis as they were the most consistent both in timing and in the delimitation of the area covered. Furthermore, in the spring, the 1-year-old fish can be separated on a length basis from the remainder of the catch. In addition the stock might be expected to have a more uniform distribution from year to year during the spring spawning season than during the summer and autumn, when the availability and abundance of food could greatly affect the distribution.

In Figure 6 the mean size of the 1-year-old Norway pout in these March surveys has been plotted against the log abundance of the total catch (predominantly 1-year-old in most years) per 10 hours' fishing, for the

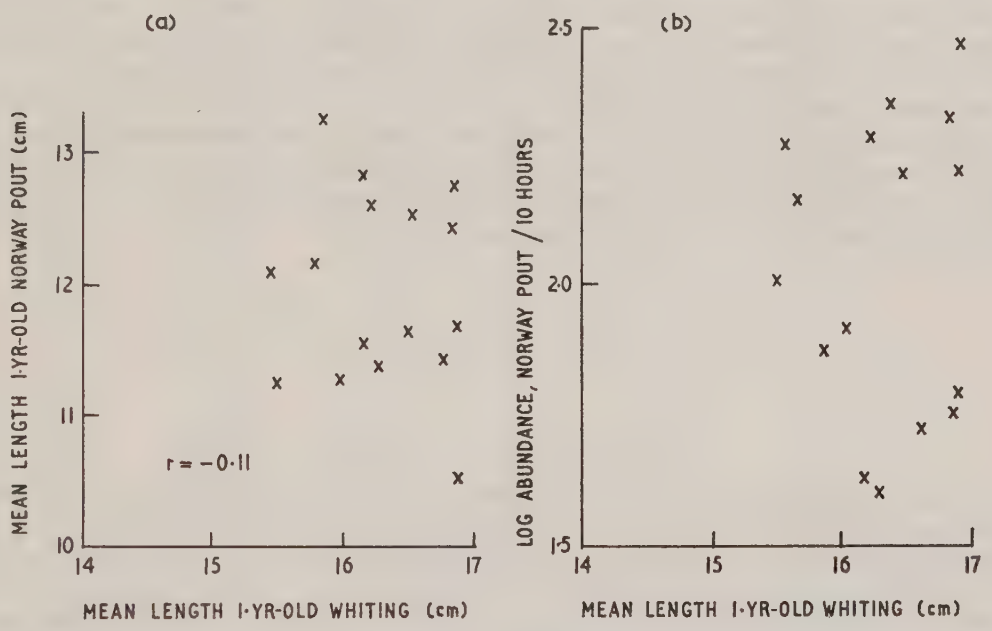

Fig. 8. (a) Mean length of 1-year-old Norway pout compared with the mean length of 1-year-old whiting.
(b) Abundance of Norway pout compared with the mean length of 1-year-old whiting.

years 1930–37, 1946–55 and 1960–66. The data for the first two periods refer to "Explorer's" catches and for the last period to "Scotia's". The available evidence points to the "Wing" trawl being, in general, substantially more efficient than the 48 ft trawl in catching these small fish. Only the "Explorer" data can be used for direct comparisons of abundance between years but there is no reason to suppose that the values for 1960–62 reflect a change in stock-size estimate from the higher figures for the previous period, and therefore there is good reason to suppose that those for 1963–66 reflect a relatively low abundance. Normally the abundance figures for the previous year would have been used, but the 1-year-old Norway pout in most years account for the bulk of the population and they are not adequately represented in the samples before they are one year old. The abundance data used, therefore, give an index of the total numbers of fish in the area while the year-class was maturing. An analysis of variance showed that the mean lengths of the 1-year-old fish were significantly different between years. Figure 6 shows that these mean lengths appear to vary inversely with the total number of Norway pout and it seems likely that growth is density-dependent. When the "Explorer" data on mean length are plotted against log abundance (Figure 7) the inverse correlation is very strong, giving a coefficient of $-0{\cdot}804$ ($P < 0{\cdot}001$): thus when abundance is high the mean length of the new brood tends to be low and when abundance is low the mean length is higher.

It is known that Norway pout are closely associated with whiting in the food cycles of the northern North Sea (Raitt and Adams, 1965). In addition to adult whiting being one of the principal predators of Norway pout, they are often found, as O-group fish, feeding on the same planktonic species (as well as being exploited by the same predators). It is interesting, therefore, to see whether the observed growth changes in Norway pout can be related to changes in the whiting stocks over the same period. When the mean lengths of 1-year-old whiting from the same "Explorer" trawling surveys in 1930–37 and 1946–55 are plotted against the mean lengths of 1-year-old Norway pout and the abundance of Norway pout respectively (Figure 8 a and b), it can be seen that in neither case is there a correlation. The mean length and abundance data for Norway pout have also been compared with the abundance of 1-year-old whiting from more limited material and no correlation was evident. It seems likely therefore that the changes in growth and abundance of Norway pout are independent of similar changes in abundance and growth of whiting in the northern North Sea.

Although feeding on planktonic species, Norway pout are mainly demersal in habit and the industrial fishery for them is to a large extent carried out with bottom trawls. Raitt (1966) concluded that they normally live close to the sea bed in daytime, but exhibit some movement away from it at night.

Information on the way in which competition may arise in the Norway pout is obscure. In the commercial fishery, when found in large concentrations, Norway pout usually constitute almost the whole of the catch (Johannesen *et al.*, 1964). In circumstances such as this competition is more likely to be intraspecific than interspecific. The situation suggests that the effects of a limitation in the food supply caused by a high density or abundance of fish might well be reflected in a decrease in growth.

MORTALITY RATES

The research ship data for northern North Sea surveys in March from 1930 to 1955 described in the last section can be used to estimate values of the instantaneous total mortality coefficient (Z). Z is composed of the fishing mortality coefficient (F) which is generated by the fishery, and the natural mortality coefficient (M) which is the loss due to natural agencies. Thus their relationship is $Z = F + M$. During the period before 1958 when there was no industrial fishery for Norway pout the fishing mortality component will have been restricted to mortalities caused by its occurring as an incidental catch in other fisheries, so that for this period it would be expected that values of Z would approximate to values of M. This is dealt with in more detail in the discussion.

Estimates of Z are obtained by converting the numbers of fish caught in each age-group into natural logarithms and averaging the differences between the same year-classes in successive years. If the mean catch of a particular year-class in successive years is A and B, then $Z = \log_e A - \log_e B$. The method used was that described by Gulland (1964). The length distributions obtained from each survey between 1935 and 1955 have been split into age categories using the age-length distributions obtained for the March 1960 survey. The results are shown in Table IV. It can be seen that the total mortality coefficient (Z) was higher between 2 and 3 years of age than between 1 and 2, or 3 and 4. The mean total mortality coefficient for all year-classes was 1·60.

The same technique has been used to calculate total mortality rates from the results of the spring surveys from 1960 to 1966. These are also given in Table IV. On average the values obtained are much higher than those for the earlier data especially in the older age groups. The mean total mortality coefficient for these year-classes was 2·75. The 2 years which gave the lowest mean values (1963–64 and 1965–66) were years when apparent negative mortalities were recorded and in the latter no 4-years-old fish were caught so that no estimate could be made. If Z is the instantaneous mortality rate then the percentage survival rate is represented by e^{-Z}. The average value of Z, 1·60, for the earlier trawling records represents about a 20% survival from one year to the next and the corresponding value of 2·75 for 1960–66 represents a 6·5% survival. The highest value obtained from this recent set of data was $Z = 6{\cdot}25$ representing a survival of only 0·2%.

TABLE IV

ESTIMATES OF Z, THE TOTAL MORTALITY COEFFICIENT (SEE TEXT), BETWEEN AGE-GROUPS. DATA FROM SPRING NORTH SEA SURVEYS

	Total mortality coefficient between ages			Mean Total Mortality Coefficient
	1–2	2–3	3–4	
1935/36	0·38	2·06	0·71	1·05
1936/37	1·05	1·78	1·54	1·45
1947/48	−0·43	2·13	0·52	0·74
1948/49	1·56	3·19	2·99	2·58
1949/50	0·22	0·84	0·65	0·57
1950/51	2·56	3·53	1·51	2·54
1951/52	1·82	2·17	2·40	2·13
1952/53	−0·27	1·35	0·25	0·44
1953/54	3·29	4·10	3·46	2·92
1954/55	1·14	1·24	0·31	0·90
Mean	1·13	2·24	1·43	1·60
1960/61	0·70	1·11	0·42	0·74
1961/62	3·15	3·91	6·81	4·62
1962/63	2·88	4·40	2·57	3·28
1963/64	−0·53	1·52	3·00	1·32
1964/65	4·61	7·93	6·21	6·25
1965/66	1·10	−0·15	—	0·31
Mean	1·82	3·12	3·80	2·75

WEIGHT AND CONDITION FACTORS

The relationship between length and weight in male and female Norway pout in a typical sample from the North Sea is shown in Figure 9. The curvilinear relationship is very steep after a length of about 14 cm is reached. There is no significant difference between the sexes. The only purpose to which information on average weight has been put in this study has been in the calculation of condition factors. The condition factor (q) is defined as $q = \frac{\text{Weight}}{\text{Length}^3}$. Only mature fish over 14 cm in length were used: the results for 1960–62 are shown in Figure 10. The results are more striking in the female fish but in both sexes condition is at its highest in the summer and early autumn, i.e. during the main feeding season, and at its lowest just after the spawning season. This is comparable with other workers' findings for related gadoids. Various attempts to assess the varying condition factors over the length range at different times of the year did not yield significant results.

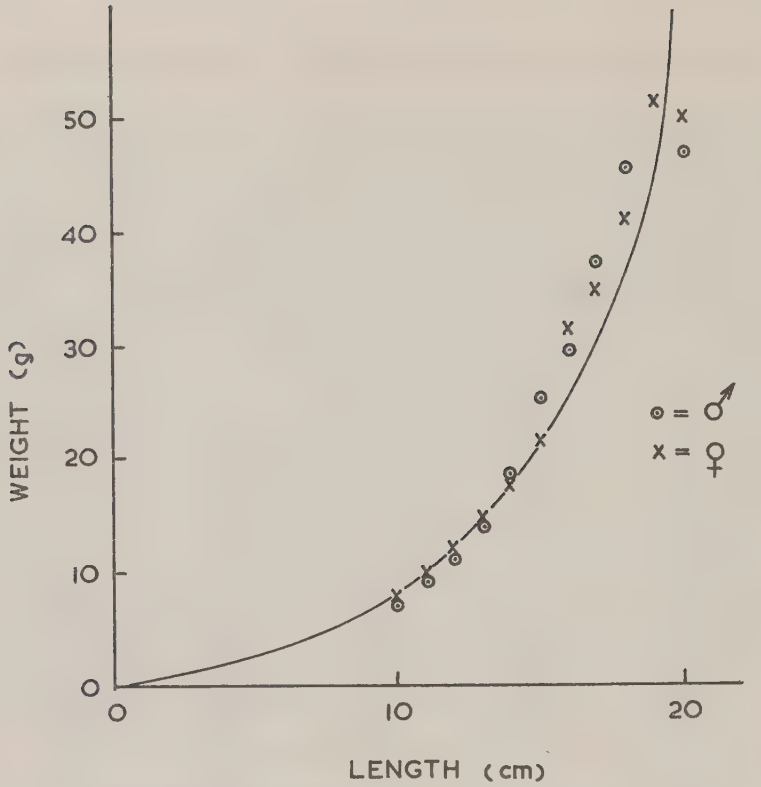

Fig. 9. Length/weight relationship in Norway pout, "Scotia", March 1962.

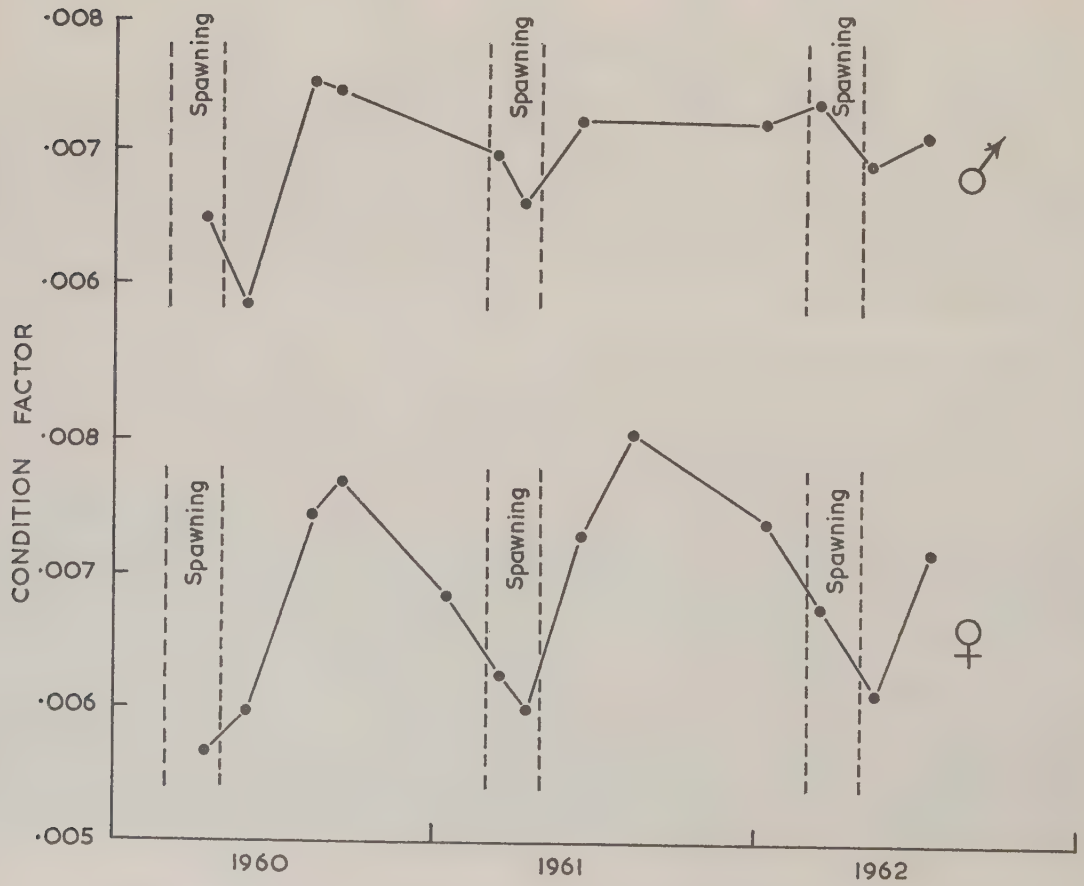

Fig. 10. Condition factors of male and female fish, 1960–62 (see text, p. 13).

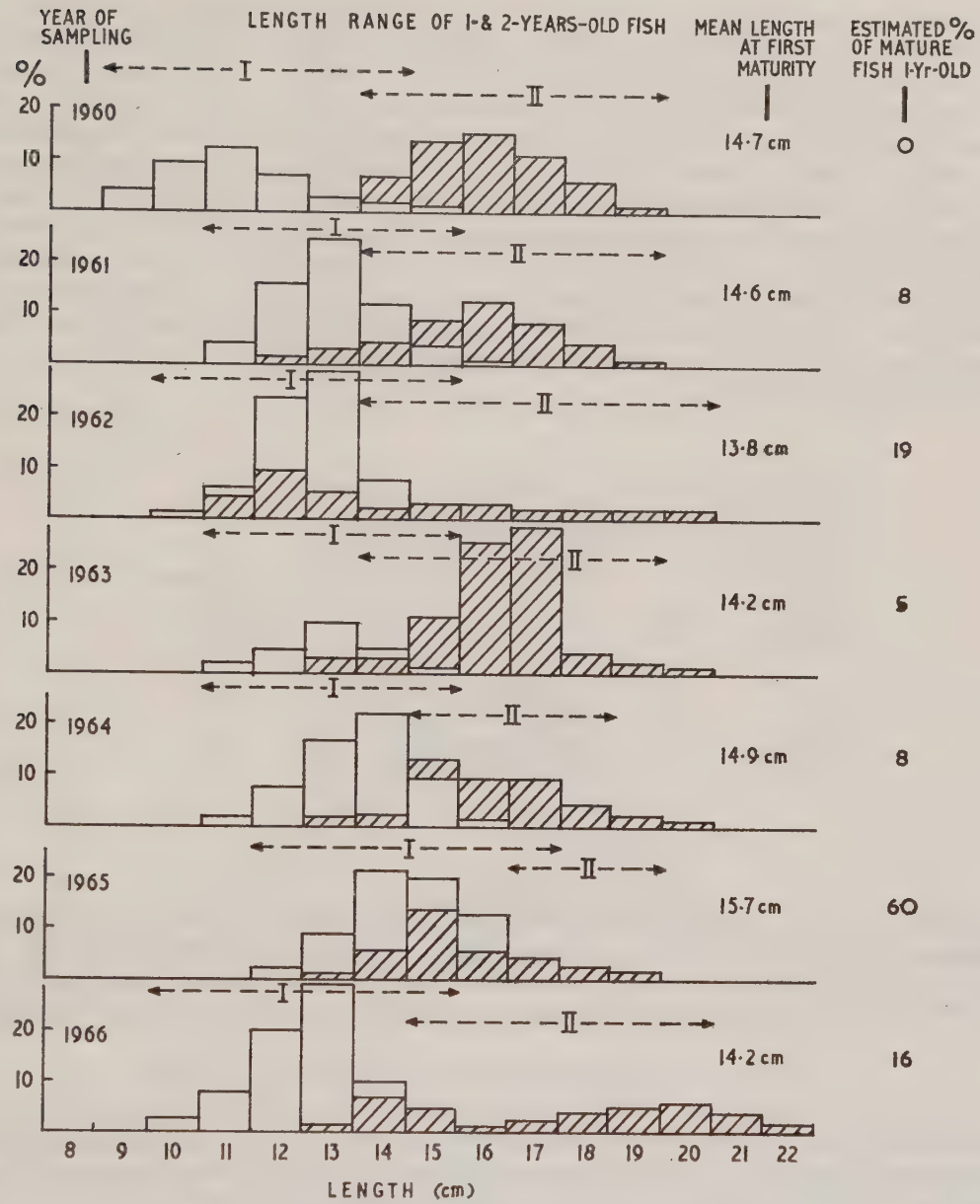

Fig. 11. Percentage maturity distribution in March samples, 1960–66.

MATURITY AND FECUNDITY

Maturity stages were recorded from samples collected during the spring surveys from 1960 to 1966. The stages used were similar to those described by Bowers (1954) for whiting, but only six stages were recognised. Bowers's stages $\frac{1}{2}$ and $\frac{3}{4}$ were combined into one maturity stage, designated $\frac{1}{2}$ in this investigation. The most detailed information is from the survey in March 1961, when the mean length at first maturity in the North Sea was about 14 and 15 cm for males and females respectively and the smallest mature individual of either sex was 13 cm. Thus it was shown that the majority of the North Sea stock spawn at two years of age, but a very

small proportion spawn for the first time when one year old. The percentages of fish (males and females combined) which were immature and mature in the spring samples from 1960–66 are shown in Figure 11. "Immature" fish were all those fish classified as immature or at stage $\frac{1}{4}$ and not likely to spawn that year. "Mature" fish were all fish at stages $\frac{1}{2}$, ripe, ripe-running and spent which were going to spawn, or had spawned, that spring. The length ranges of 1-year-old and 2-years-old fish, the mean length at first maturity and the estimated percentage of mature fish which were 1-year-old are also shown in Figure 11. In the samples from 1960 to 1964 only small numbers of 1-year-old fish were mature, but in 1965, 60% of the 1964 year-class were potential spawners. In 1965 also, the length range of the 1-year-old fish was higher (from 12 to17 cm as compared with about 10–15 cm in other years). The 1964 year-class is that which was growing up in conditions of very low density, since the previous year-class in 1963 had been exceedingly poor. The mean length at first maturity did not change appreciably during the overall period, although it was rather higher in 1965. However, the length range over which the maturity change takes place is so short that it is difficult to estimate the 50% point with precision.

TABLE V

SOURCES OF FECUNDITY MATERIAL

Year of sampling	Age of fish	Area	No. of fecundity estimations obtained
1964	2	Scalloway Deeps (west side of Shetland)	48
1965	1	Fladen ground	29
1966	2	Fladen ground	76

The fecundity of a fish is usually defined as the number of mature eggs in the ovary before spawning. Some information on fecundity is available for comparing the 1964 year-class with that of 1962. The sources of the material used for the fecundity work are given in Table V. The fish were preserved in formalin and examined in the laboratory. A shrinkage experiment was carried out and the relationship was found to be:

$$\text{fresh length} = \text{length after preservation in formalin} \times 1{\cdot}0262$$

The eggs were found to be reasonably easy to sort into two main groups: (1) ripening eggs due to be shed at the next spawning period and (2) very small eggs probably due to be shed at some future spawning. This is as described by Raitt (1933) for haddock, and only the eggs to be shed at the next spawning were counted. On some occasions large hyaline eggs were also encountered in the samples and since this could indicate that some eggs had already been shed, ovaries containing these eggs were not used in the investigation. Samples of eggs were measured using a micrometer scale in the eyepiece of a binocular microscope. The scale was such that one microscope eyepiece unit measured 0·064 mm. The length measurements of samples of eggs from two ovaries are shown in Figure 12. The very small eggs (2, above) were less than one e.p.u.

The ovaries were cleaned and all connective tissue was removed. The eggs were separated and placed in water, and the volume was made up to 200 ml. After careful mixing by non-rotary stirring, a 1 ml sample was extracted by a Stempel pipette. The data obtained in this way have been checked statistically to confirm that there was even mixing and that random samples were being obtained. To ensure that each count was measured to the same degree of accuracy, different numbers of pipette samples were taken. When the ovary was small, two or three such subsamples were sufficient to give an accurate estimate of total numbers. As the size of fish and numbers of eggs in the ovary increased, up to five subsamples had to be taken.

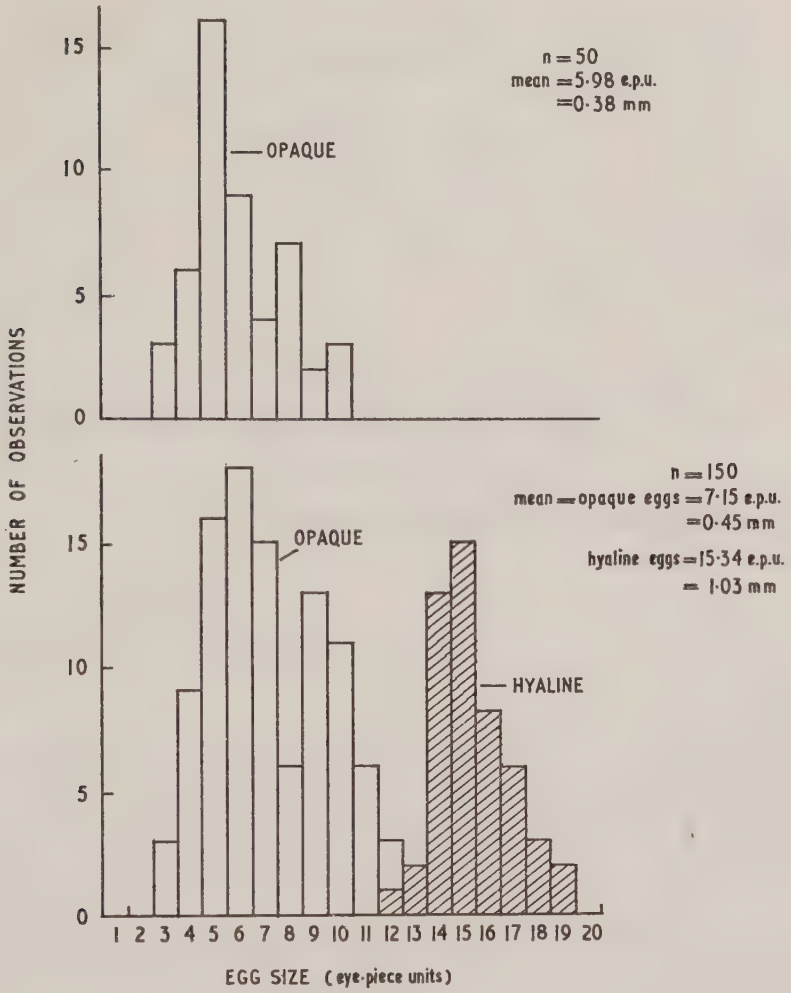

Fig. 12. Egg size in Norway pout ovaries.

The estimated egg counts obtained were analysed statistically to determine the relationship between the fecundity and the size of fish. It is customary to take length as the index of size in fecundity relationships since it can be determined more accurately under widely varying conditions (e.g. at sea) than other measurements such as weight. This procedure was followed in this investigation. The relationship between fecundity and length in other species has been found to be curvilinear, of the form:

$$F = aL^b$$

where F = fecundity and L = length in cm. The parameters a and b are estimated from the data by determining the regression of log F on log L, the relationship on the logarithmic scale being linear. When this relationship was fitted to the three samples the following results were obtained:

1-year-old in 1965	$\log F = 4{\cdot}2545 \log L - 0{\cdot}6838$
2-years-old in 1966	$\log F = 2{\cdot}7038 \log L + 1{\cdot}2514$
2-years-old in 1964	$\log F = 3{\cdot}6628 \log L - 0{\cdot}3735$

The distribution of the fecundity observations plotted as log fecundity on log length are shown in Figure 13 a and b (1-year-old fish of 1965 and 2-years-old of 1966) and in Figure 13 c (2-years-old fish of 1964).

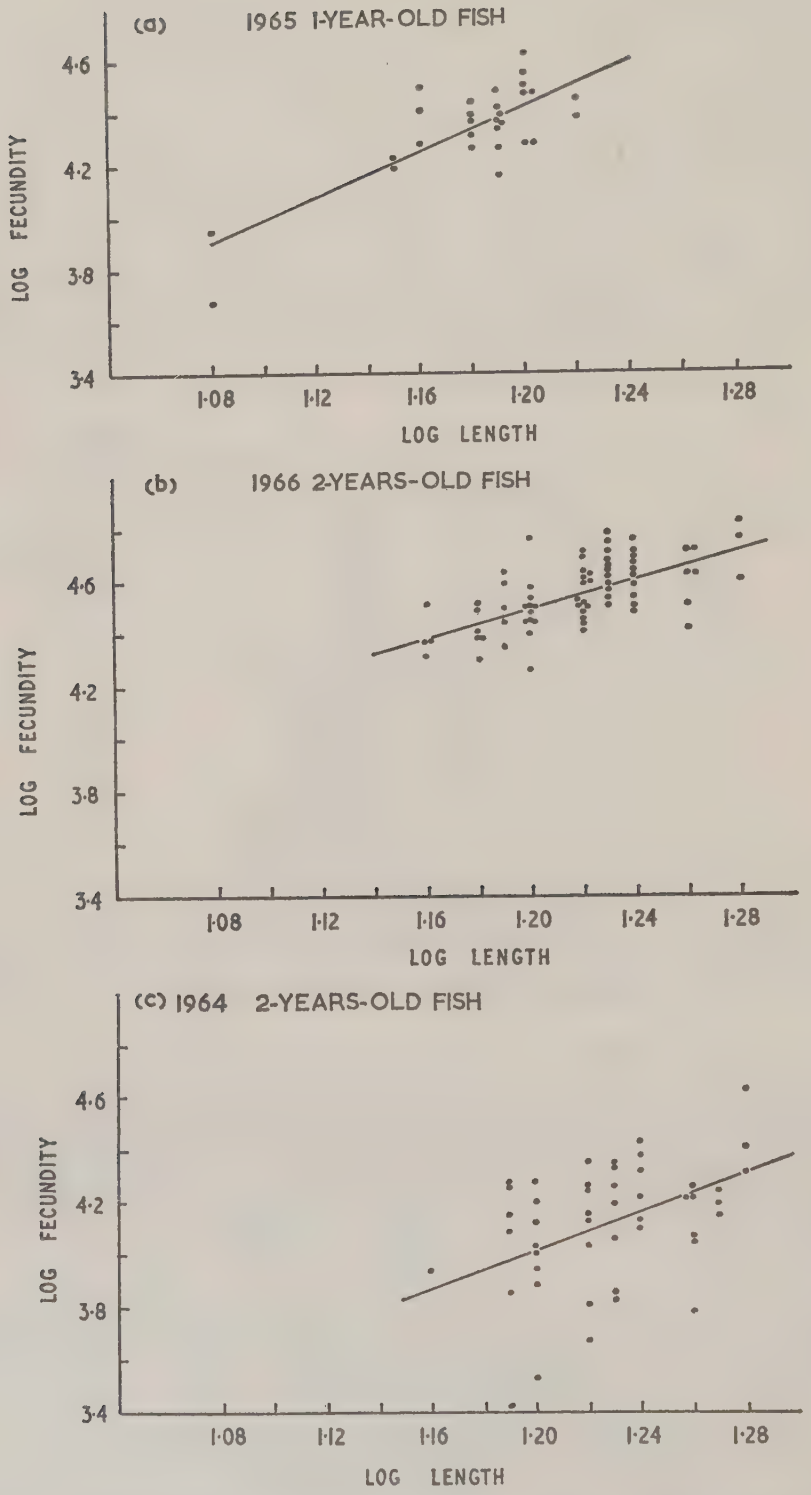

Fig. 13. Fecundity-length relationship; (a) 1-year-old fish in 1965; (b) 2-years-old fish in 1966; (c) 2-years-old fish in 1964.

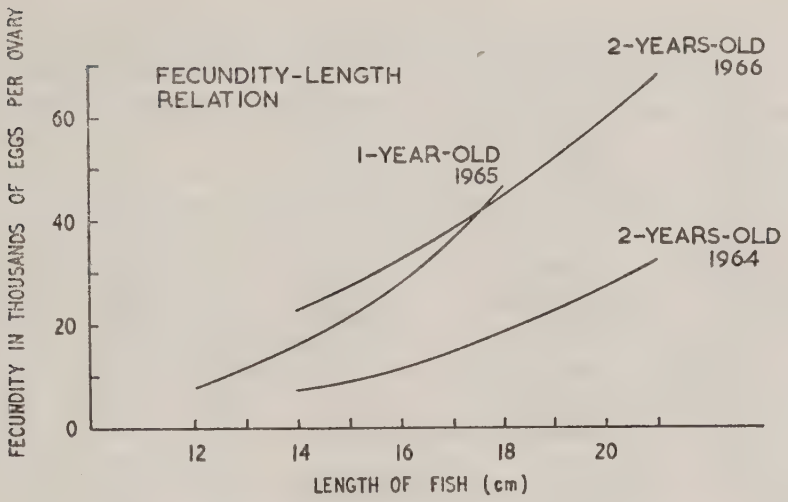

Fig. 14. Comparison of all three sets of fecundity-length data.

There are very wide variations in the range of fecundity estimates at any one length. The proportion of the total variation in log F accounted for by variation in log L in the above equations was 40%, 60% and 20% respectively. This last figure for the 2-years-old Norway pout in 1964 is very low indeed and it seems clear that, in addition to length, other factors, at present unknown, cause this high variability. The gutted weights of the 2-years-old fish in 1964 were introduced as a possible additional explanatory variable, but this did not lead to an improvement in the amount of variation of log F accounted for.

The fecundity-length relations from the three sets of data plotted together on the original scale are shown in Figure 14. The lines from the 1-year-old fish in 1965 and those which were 2-years-old in 1966 are fairly similar—they both refer to the 1964 year-class. The relationship in 2-years-old fish in 1964 is quite different, however, and the fecundity at any given length is lower by a factor of from 2 to $2\frac{1}{2}$ times.

The above relationships are to estimate log fecundity given log length, and are used in the comparison of data. The logarithmic transformation, however, introduces a bias, so that the equation in this form will always underestimate the expected number of eggs. To overcome this bias a correction equal to $1{\cdot}15\left(\frac{n-1}{n}\right)s^2$ has been applied, where s^2 is the residual variance of the log values and n is the number of observations in each mean. The relationships for estimating the expected number of eggs at a given length, with this correction applied, are:

1-year-old in 1965	$\log F = 4{\cdot}2545 \log L - 0{\cdot}6698$
2-years-old in 1966	$\log F = 2{\cdot}7038 \log L + 1{\cdot}2618$
2-years-old in 1964	$\log F = 3{\cdot}6628 \log L - 0{\cdot}3245$

The expected numbers of eggs at centimetre length intervals are shown in Table VI. Apart from the clear differences between the two samples of 2-years-old fish, within each of the two sets of results it can be seen that for an increase in mean length of 2 cm the fecundity is increased by a factor of about 1·5. The range of mean lengths of 2-years-old fish in March from 1960 to 1966 was 16·02–18·92 cm.

TABLE VI

ESTIMATED NUMBERS OF EGGS FOR FEMALES OF A GIVEN LENGTH

Length (cm)	2-years-old fish 1964	1-year-old fish 1965	2-years-old fish 1966
12	—	8,337	—
13	—	11,750	—
14	7,464	16,070	22,910
15	9,616	21,530	27,610
16	12,190	28,380	32,890
17	15,170	36,560	38,640
18	18,710	46,770	45,190
19	22,910	—	52,480
20	27,610	—	60,120
21	32,960	—	68,550

DISCUSSION

The Norway pout is known to be one of the most abundant gadoids in the northern North Sea. The age-composition of the population has been described in this report. It consists principally of one or two year-classes and very few fish over 3 years of age are found. Normally the spawners each spring are 2-years-old fish.

Other abundant North Sea gadoids such as cod, haddock and whiting show large fluctuations in individual year-class strengths, but the effect of these fluctuations on the total adult stock is usually evened out by the presence of several year-classes in the population, so that poor survival in certain years tends to be compensated for by good survival in others. Since the stock of Norway pout in the North Sea is composed mainly of one or two year-classes and few fish survive to spawn more than once, one would expect that the stock would be particularly liable to large scale fluctuations in year-class strengths. The population characteristics of a species like the Norway pout need to ensure a rapid replacement of the stock —e.g. fast growth and early maturity. On the other hand long-lived species usually mature later and the recruitment each year represents a smaller proportion of the total population.

One of the main contributors to the relatively high total mortality of Norway pout appears to be predation, since they are known to be the prey of whiting (Jones, 1954), cod (Graham, 1923) and megrim (Rae, 1963) in the northern North Sea.

Ursin (1963) has observed that there are anomalies in the seasonal variation of the growth parameters which suggest that physiological stress may be an important component of the natural mortality of Norway pout. Beverton and Holt (1959) point out that the annual weight variation in a fish approaching its asymptotic length (L_∞) is due predominantly to the production and shedding of sexual products, which must cause a loss in condition with age and possibly mortality. The values of L_∞ obtained in this report were 18–19 cm, which are within the length range of 2-years-old fish in recent years. Beverton and Holt (1959) also draw attention to the apparent positive correlation between the coefficient K of the Bertalanffy growth equation and the instantaneous natural mortality coefficient M in many families of fishes, including the gadoids. Using their graph (their Figure 6), the values of K for Norway pout would give a natural mortality coefficient M of between 1·1 and 1·3. This is very high compared with the figures for the larger gadoids; the natural mortality coefficient of cod, for instance, is usually taken to be about 0·2. However, it is of the same order of magnitude as the estimate of Z obtained for the years prior to the industrial fishery (p. 12). In the section on mortality rates it was suggested that during this period Z would be expected to approximate to M. The value of Z obtained for these years was 1·6.

From a long series of data, growth in Norway pout during the first year of life has been shown to vary inversely with stock abundance. It appears likely that food is one, but not necessarily the only, limiting factor to growth. The available evidence suggests that Norway pout normally inhabit a zone just clear of the sea-bed and feed on the deepest layers of plankton just off the bottom. In this "ecological niche" there is more likelihood of intraspecific than interspecific competition.

It is appropriate now to consider the changes in the North Sea population during the period for which detailed information is available (1960–66). The "normal" situation for the early years appears to have been that the spawning population consisted mainly of 2-years-old fish and a few maturing at one year. The 1963 year-class was very poor. This and the two succeeding year-classes, which were also poor, all grew faster, so that length at particular ages increased by about 10% (or 1·5 cm) compared with earlier years. About 60% of the 1964 year-class were mature at one year of age and most of the spawners in 1965 were one year old. The 1964 year-class was growing during the period when the poor 1963 year-class made up the adult population, i.e. when the adult stock was at a very low density. As 2-years-old fish in 1966 their mean fecundity at a given length was 2 to $2\frac{1}{2}$ times higher than the corresponding value for the 2-years-old fish in 1964. While there is always the possibility that this result might have arisen from biased or inadequate sampling, the results are based on a fairly large number of samples and it is most unlikely that any discrepancies in sampling could have given rise to differences of this magnitude. Thus the fecundity-length relationship is not constant from year to year. Under conditions of extremely low stock abundance not only was there a significant increase in growth, which would increase the egg production potential of individual fish, but over and above this the fecundity of fish at a given length increased by 2 to $2\frac{1}{2}$ times. It is important to note that, although there was a significant lowering in the age at first maturity, the length at first maturity remained about the same.

Changes between years in fecundity of fish of the same size have also been reported for other species. Chugunova (1951) demonstrated this feature in semi-migratory carp for the North Caspian Sea, and to a less extent Nikolskii and Belyianina (1959) have done so in North Sea herring. In neither of these examples, however, was the increase as great as $2\frac{1}{2}$ times. Nikolskii (1962) has stated that fecundity increases of this type can be reached "either by an increase in the volume of the gonads or by a decrease in egg size. In the latter case, if the density of the yolk and the amount of fat in the yolk do not increase, some decrease of food supply for the developing organism takes place during its feeding on the yolk". Unfortunately I have no information on ripe egg size from the material examined since all the ovaries were at the $\frac{1}{2}$-ripe stage with no hyaline eggs present. However, it may be relevant that the 1-year-old Norway pout in 1965, which had nearly as high an individual fecundity at the lower length sizes as the 1966 2-years-old fish, gave rise to the poorest year-class (1965) in the 7 years investigated. It is not impossible that those fish spawned in 1965 were the products of larger numbers of smaller eggs.

The implications of these results require careful consideration. The abundance of the population is inversely related to growth, and fairly small increases in growth will, on average, increase the fecundity significantly. This situation will, at low stock densities, substantially increase the average number of eggs per fish. This could be a fortuitous result. It could, however, be some form of built-in mechanism, which ensures that when Norway pout are fewer they are larger and have a higher fecundity, and that when there are many they are smaller and have a lower fecundity. This in turn might ensure that the spawning potential each year would be big enough to withstand some of the extremes of larval mortality which appear to give rise to the major fluctuations in brood strengths of most other marine fishes. While it seems more likely that this latter hypothesis is correct than that the result is purely fortuitous, it is difficult to see where the very large increase in individual fecundity at a given length demonstrated for the 2-years-old fish in 1966 fits into the general picture. If this increase in egg numbers is at the expense of the quantity of yolk in the egg it may be detrimental to egg survival and hence have a disadvantageous effect on the potential year-class strength. It is, therefore, especially unfortunate that no data on egg sizes are available.

So far consideration has been given only to the way in which recent changes in the dynamics of the stock could have been affected by natural causes. The quantities caught by the industrial fishery in some years have been enormous (see Appendix). In 1963, for instance, the catch was 188,000 metric tons. If the average weight of a Norway pout is taken as 25 gm this represents a total of 75×10^8 fish. No detailed statistics are available on fishing effort or catch-per-unit effort in this fishery, nor are there details of the length- and age-compositions of the landings. Furthermore, there is no information on the total stock size in the northern North Sea, but the removal of such a large number of fish is bound to have some effect on the population. The examination of the changes in the total mortality coefficient $Z\ (=F+M)$ is not much help in this context as the possibility of an increase in the natural mortality component (M) associated with the physiological stress

of maturing at an earlier age cannot be dismissed. In other words, fluctuations in Z during the period investigated cannot be assumed to have been caused by increased fishing (F) alone. On the other hand, there has been no significant change in the value of the coefficient K from the Bertalanffy growth equation, which is believed to be related to the natural mortality rate. It is possible that an active migration of older fish away from the North Sea area could have resulted in an increase in the apparent natural mortality but it is difficult to see why this should now occur when there has been no evidence of it in the past (Raitt and Mason, 1968). It would appear, therefore, that there is more evidence at this stage of the increase in total mortality being attributable to fishing than to a rise in the natural mortality rate, whether apparent or real.

The reduction in the landings of Norway pout in the industrial fishery from 1963 (188,000 metric tons) to 1965 (77,000 metric tons) is probably associated with the low abundance recorded in the present analysis of research ship trawling data for those years, and with the occurrence of the poor 1963 year-class. By 1966 Danish vessels were having to trawl as far afield as west of Orkney and west of the Hebrides to catch Norway pout since there were insufficient quantities in the North Sea (K. Popp Madsen, personal communication). The results of research surveys in the North Sea in March 1967, however, suggest that catching rates are now much better and that the strength of the 1966 year-class is average.

To conclude, then, Norway pout is a short-lived, fast-growing species, and would appear to be very vulnerable to large-scale fluctuations in individual brood-strengths. During a period when a very poor year-class was joining the North Sea stock the population had also been exploited by an industrial fishery. The relationship between growth, age at first maturity, individual fecundity and total egg production potential appears to be variable under conditions of changing abundance, and it seems logical to assume that this is an adaptation by which a species with a short life-span, like the Norway pout, can restrict its fluctuations in numbers. The present indications are that the population has begun to recover from a period of very low abundance, possibly helped by its own population control mechanisms and a reduction in the fishing effort.

SUMMARY

Otoliths were used for determining the age of Norway pout. Very few fish over 3 years of age were found and the population generally consisted of only one or two year-classes. Estimates of abundance of different year-classes in trawling surveys from 1960 to 1966 showed that over this period there occurred a remarkable drop in the population numbers of Norway pout in the northern North Sea. The 1963 year-class was the poorest for five years and the 1965 year-class appeared to be even poorer.

Data on length showed that the decrease in numbers had been associated with a 10% increase in the length of fish at the same age. This growth increment appeared to have been gained in the first year of life. The examination of a long series of past trawling records demonstrated that the mean lengths of 1-year-old fish each spring varied inversely with the total number of Norway pout and it seems likely that growth is density dependent. The possibility of food being the limiting factor is discussed.

Estimates of the instantaneous total mortality coefficient Z were higher for the period 1960–66, when there was a fishery for Norway pout, than for earlier years.

From an examination of the relationship between weight and length, the condition of the fish was found to be highest during the main feeding season and lowest just after the spawning season.

Maturity and fecundity information is presented for the years 1960–66. Sixty per cent of the 1964 year-class, which were juvenile fish during the period when the very poor 1963 year-class made up the adult population, were mature when 1 year old instead of at the more normal age of 2 years. A comparison of the mean fecundity of 2-years-old fish of the 1962 and 1964 year-classes, at a given length, showed that the estimates for the latter were higher by a factor of 2 to 2½ times.

The effect of the industrial fishery for Norway pout in the North Sea and of the changing mortality coefficients in the period investigated are briefly discussed.

The changes in the characteristics of the population which followed the advent of the poor 1963 year-class were very striking. The relationship between density-dependent growth effects and age at first maturity, individual fecundity and total egg-production are considered. It seems logical to conclude that this is an adaption by which a species with a short life-span, like Norway pout, can restrict its fluctuations in numbers.

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APPENDIX

A SHORT NOTE ON THE INDUSTRIAL FISHERY FOR NORWAY POUT IN THE NORTH SEA

The stocks of Norway pout in the North Sea are exploited by an industrial fishery for the production of animal feeding stuffs and fertilisers. At present only two countries take part in this fishery, Denmark and Norway, but from small beginnings in 1958 the total annual catch rose to a record 188,000 metric tons in 1963. No statistics are available for 1958 but the annual landings from 1959 to 1965 are shown in Figure 15. The reduction in landings in 1960 and 1961 was associated with a decrease in fishing owing to the general low level of fish-meal prices in those years. It is interesting to note that, whereas Denmark dominated the fishery for the first 4 years, Norway landed almost twice as much as Denmark in 1964. Since 1963 there has been a decrease in the total landings although to some extent this may have been affected by changes in fishing effort.

The Danish vessels which catch Norway pout belong to the industrial fishing fleet which exploits the young herring stocks in the central North Sea in the spring and autumn and sand eels in the summer. The

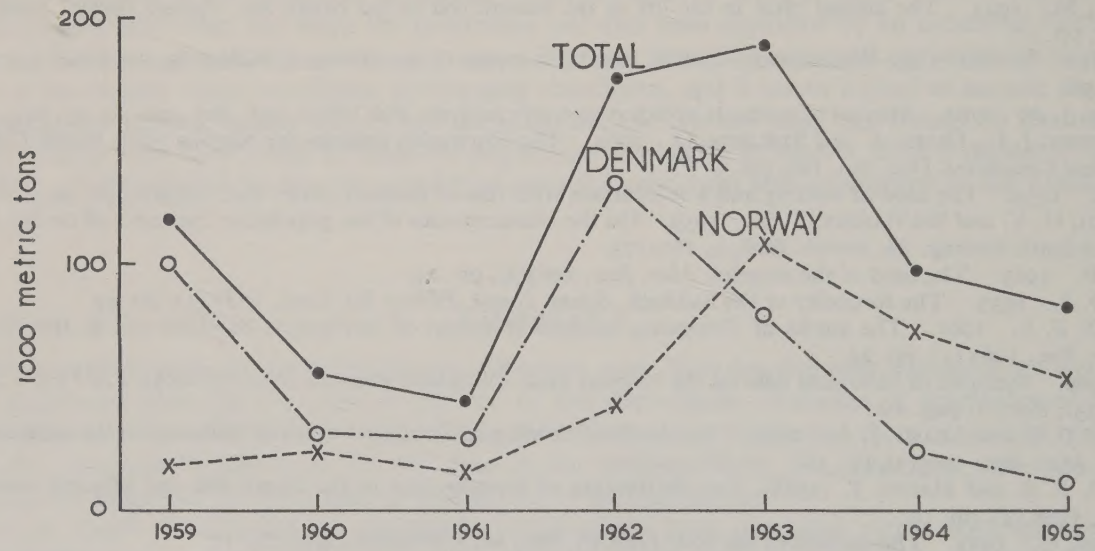

Fig. 15. Annual landings of Norway pout from the North Sea.

fishery for Norway pout was first started in the winter months and filled the gap between the autumn and spring herring fisheries. Most of the Danish vessels are based at Esbjerg and are relatively small wooden cutters between 60 and 90 ft long, although a few are steel vessels of up to 110 ft.

The bulk of the Norwegian and Danish catches is taken in the northern North Sea, although there is some fishing in the Skagerrak. Fishing is mainly carried out at depths of 50–150 fm (91-274 m), and in general the grounds fished have a fairly smooth sand-mud bottom. The gear employed is a special, small-meshed, wing-type trawl of synthetic material with a light groundrope. The trawl doors are also light and long spreading wires from the doors to the wings are favoured.

The Danish fishery in the North Sea mainly covers the area from the Devil's Hole northwards to the Fladen ground: in November 1962, the research ship "Scotia" worked for a few days alongside the Danish fleet in this area. From information gathered on the vessels at this time, it appeared that they were taking up to four days to fill up with fish before setting off on the 360 miles' journey back to Esbjerg.

The Norwegian fishery covers a rather larger area and the most important grounds fished are the Fladen, Bressay Shoal, Viking Bank, The Patch and Egersund Bank. The main fishery is now from April or May to October, the winter fishery being less important. Some of the Norwegian vessels are pair trawlers.

The available data from these fisheries suggest that the by-catch of protected species is generally low.

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